

Implicit learning is too fast to be a slow process

Jennifer E. Ruttle*^{1,2}, Bernard Marius 't Hart^{1,3} and Denise Y. P. Henriques¹⁻³

¹Centre for Vision Research, York University, Toronto, Canada

²Department of Psychology, York University, Toronto, Canada

³School of Kinesiology and Health Science, York University, Toronto, Canada

*** Corresponding Author**

Jennifer E. Ruttle

Email: jennruttle@gmail.com

Abstract

In motor learning, the slow development of implicit learning, following explicit components of learning is well established. While much is known about behaviour during adaptation to a perturbation in reaches, saccades and locomotion, little is known about implicit processes during adaptation. Implicit learning is characterized by both changes in internal models and state estimates of limb position, which we measure as reach aftereffects and shifts in hand localization, after every training trial. This allows trial-by-trial mapping of implicit learning. Participants reached to targets with aligned, then 30° rotated, counter-rotated and finally error-clamped cursor feedback. This paradigm allows fitting a common state space model to the reach performance. The slow process of the model did not match the time course of either of our implicit measures. The observed implicit changes were near asymptote after only one perturbed training trial and thus occur much faster than conventionally believed.

Introduction

An established convention of motor learning asserts that automatic or implicit components of learning emerge later in training following an initial more explicit or declarative stage, even for skill maintenance tasks, like adaptation (1–5). Here, we show that implicit changes during reach training occur immediately and do not require prolonged training at all.

Two main implicit changes involved in adaptation, that rely on sensory-prediction error-based learning, are updates in internal models as well as the resulting changes in our state estimates (6–8). While perturbations in reach, saccade and locomotion adaptation evoke relatively quick adjustments to behaviour (4,9–12), it has not been directly measured how quickly implicit changes emerge.

One hallmark of implicit learning: reach aftereffects, is the persistence of motor changes even when the perturbation is removed, which is thought to reflect a change in internal models during adaptation (7,13). Another implicit change involves shifts in our perceived hand location or state estimate, to reduce the discrepancy between where the participant sees and feels their hand (6,14–18). It is thought that implicit learning arises slowly with exposure to a perturbation along with explicit components of learning (1,2,19). Our lab has shown that reach aftereffects and shifts in hand localization emerge after 6 trials (20,21). In the current study, we push this further by having participants alternate between training and testing trials, while adapting to a 30° rotation, its reversal and then error-clamped trials. Each group of participants performed one type of testing trial that could assess either changes in state estimates or internal models. By probing implicit changes after each training trial, we increase the resolution of measuring implicit changes greatly.

We compared the time course of the various implicit changes we measure with the two processes of state space models that have been used to describe the time course of adaptation (22). The fast and slow process of these state space models have

been suggested to map onto explicit and implicit components of learning respectively (19). Hence, here we compare the model processes to our measures of implicit learning. We find changes in reach aftereffects and state estimates to be much faster than the models' slow processes. State estimates asymptote after a single trial and are best described as a proportion of the perturbation. In short, our results challenge the convention that implicit learning is slow, and show that some implicit changes emerge before, and likely separate from, explicit changes in motor control.

Results

Hand localization experiment

96 participants adapted to an imposed perturbation interleaved with test trials or a short pause in time. The test trials involved measuring estimates of the hand location after the trained hand was displaced by a robot manipulandum (passive localization, Fig 1A&D) or by the participant themselves (active localization, Fig 1A&C). A third control group had no measurements of hand location and instead just paused during the allotted time (Fig 1A). Comparing these three test-trial groups (passive, active and pause) we can investigate learning-induced changes of hand estimates across training. We begin by analyzing the reach training performance and fitting the two-rate model, to reach performance (22). We then compare the model processes to the passive and active hand localization shifts which measure components of implicit learning.

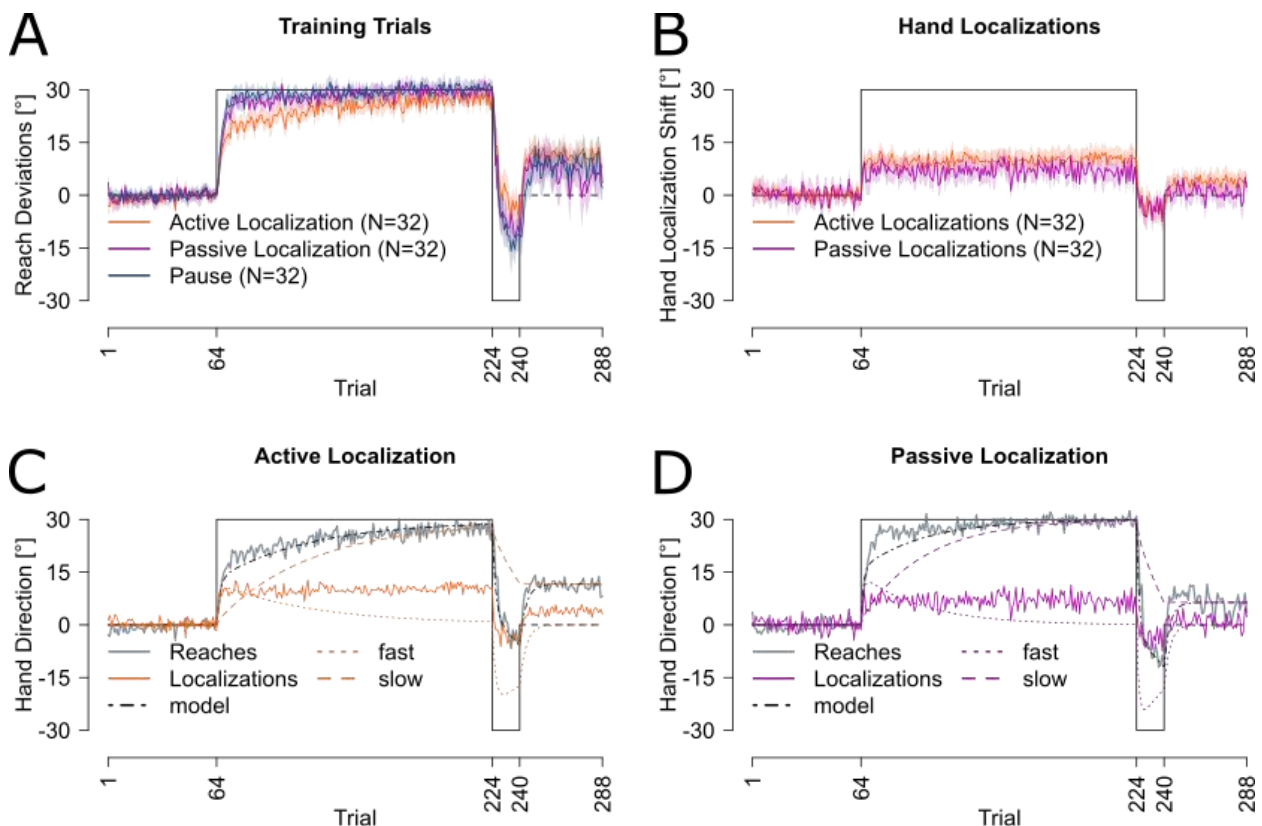


Figure 1. Performance across measures for passive, active and pause groups. **A:** reach training performance averaged across all participants for each corresponding group. **B:** Hand localization performance for the two groups. **C&D:** Model predictions for the active and passive localization groups. All solid lines are an average of all participants in that group, shaded regions are 95% confidence intervals. Trials included in analysis are as follows: R1=trials 65-68; R1_Late=trials 221-224; R2=trials 237-240; EC=273-288.

Training Trials

To investigate whether the type of intervening test trial affects training performance (Fig 1A), we conducted a mixed ANOVA with group (passive, active or pause) and trial set (R1, R1_Late, R2 and EC, described in figure 1 & 5). As expected, reach deviations varied across trial set [$F(3,279)=537.99$, $p<.001$, $\eta^2=.80$], and there was a significant interaction between trial set and group [$F(6,279)=8.29$, $p<.001$, $\eta^2=.11$], but no effect of group on its own [$F(2,93)=1.90$, $p=0.15$]. Follow-up ANOVAs show that learning was slower in the active localization compared to the other conditions [all $p<.001$].

Model Fitting for Training

We fit the two-rate model (22) to the averaged reach deviations for each group (see figure 1C&D). The model (black line) does a rather good job at predicting the average performance (grey line). As shown in table 1, the learning rates for the active group are slightly lower than the passive or pause group, in line with results above. Importantly, the retention parameters are very similar across all three groups, indicating the same ability to retain what was learned. In summary, despite an interesting effect of test-type, reach-training performance was similar enough to compare performance on these hand localization test-trials.

Group	Rs	Ls	Rf	Lf	MSE	twoRate AIC	oneRate AIC	oneRate likelihood
Active Localization	0.999	0.030	0.760	0.158	4.053	15.605	27.004	0.003
Passive Localization	1.000	0.054	0.740	0.236	7.425	19.548	27.207	0.022
Pause	1.000	0.055	0.825	0.226	8.345	19.293	25.697	0.041
No-Cursor	0.991	0.036	0.735	0.151	3.125	14.012	19.195	0.075

Table 1. Model parameters and goodness-of-fit estimates. All twoRate AIC's are smaller than respective oneRate AICs indicating a better model fit from a two-rate model. Relative likelihoods below .05 are bolded.

Test Trials

We also compare the time course of changes in estimating the location of the unseen, adapted hand across training: for the passive vs. active localization shown in Fig 1B. Estimates of hand position show a rapid shift on the first trial after the initial perturbation is introduced for both active 8.95° [$t(31)=12.49$, $p<.001$, $d=2.21$, $\eta^2=.70$] and passive localizations 6.46° [$t(31)=6.32$, $p<.001$, $d=1.12$, $\eta^2=.32$]. These shifts do not increase with further training [all $p>.05$], indicating hand localization shifts asymptote after a single trial.

Despite similarly quick shifts in hand localization (Fig 1B), a mixed ANOVA revealed a significant difference in hand estimates between the active and passive localization groups [$F(1,62)=6.28$, $p=0.014$, $\eta^2=.05$], across trial sets [$F(3,186)=96.97$, $p<.001$, $\eta^2=.43$] and an interaction between trial set and group [$F(3,186)=2.93$, $p=0.04$, $\eta^2=.02$]. Follow-up t-tests indicate larger shifts in felt hand position in the active localization group both during the initial [$t(51.43)=2.37$, $p=0.022$, $d=.59$, $\eta^2=.08$, 2.92°] and final [$t(61.78)=2.98$, $p=.004$, $d=.74$, $\eta^2=.11$, 4.35°] trial set of the first rotation and at the end of the error clamp phase [$t(61.99)=2.73$, $p=.008$, $d=.68$, $\eta^2=.11$, 3.5°]. Thus, even though the participants in the active localization paradigm seemed to learn slightly slower than the passive group, they showed a slightly larger shift in felt hand position, except during the counter rotation [$t(58.93)=-0.15$, $p=.88$]. This separation between active and passive localization shifts reflects the role of predicted sensory consequences in state estimates of hand position and more generally, motor learning.

Alternative to Two-Rate Model

Given that shifts in hand localization did not mimic the observable pattern of either the fast or slow process, we next tested whether changes could simply be described by the perturbation size alone. In previous studies, change in felt hand position was usually 20-30% of the perturbation (15,23,24). Indeed, when the changes in hand position were fit with a linear regression estimating the proportion of the perturbation accounted for (passive: ~20% active: ~35%), we see a reasonable fit between actual hand location estimates and these simple models (see figure 2A-C). Similar regression estimates (black line) are used as the proportion of the perturbation that hand estimates would have shifted and compared to the actual data (colored lines) shown in figure 2D&E. In combination with the sudden change in localization, these results suggest that localization shifts involve a perceptual recalibration that does not require slower adaptation or learning and may guide adaptation, rather than follow from it.

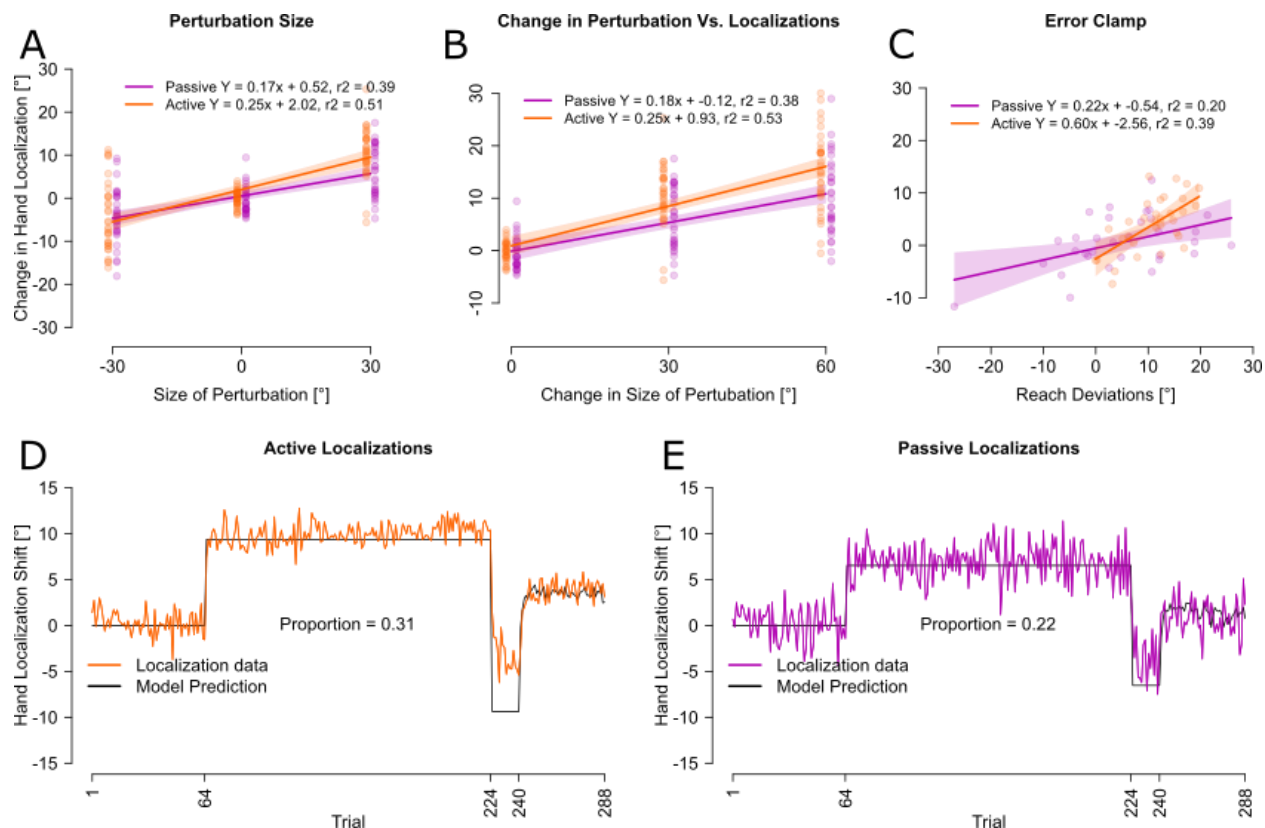


Figure 2. Regression and proportional fits between localization and error clamp trials. **A-C:** Regressions between localizations and either the size of the perturbation, the absolute change in size of perturbation and the participants average performance on the final 16 error clamp trials. The shaded regions represent the 95% confidence interval around the regression line. **D-E:** The proportional models' prediction and the averaged participant performance for each localization test trial separately.

Reach aftereffects experiment

Next, we measured the time course of changes in no-cursor reaches or reach aftereffects at the same scale. We began again by investigating whether these test trials affected reach-training performance like we did for hand localization and included the pause-group as our control again. Figure 3A shows the reach training performance for both groups, with their 95% confidence intervals. We also include the model fit and the no-cursor reach trials in figure 3B.

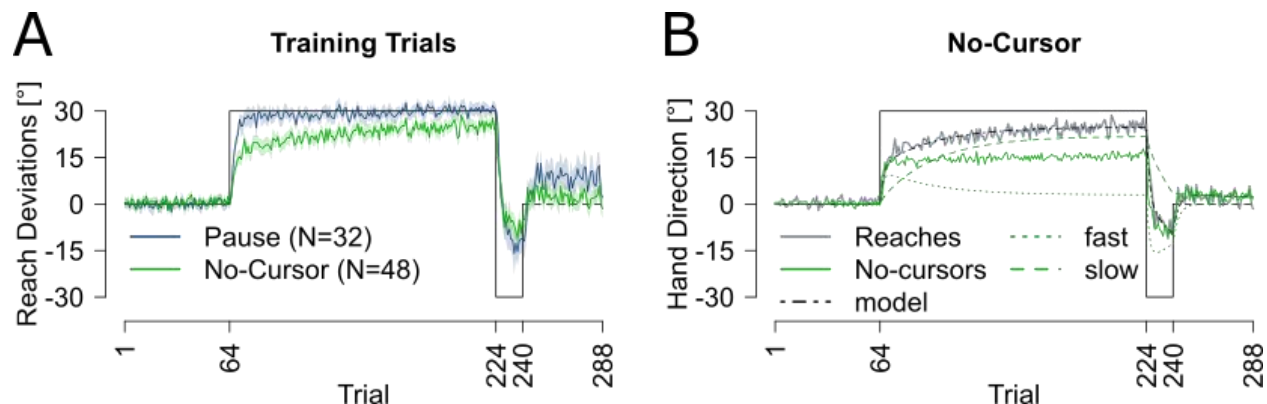


Figure 3. Performance across measures for pause and no-cursor groups. **A:** Reach training performance averaged across all participants for each group. **B:** Two-rate model fit (black and green dashed lines), reach performance (grey line) and no-cursor test trials in solid green. All solid lines are an average of all participants in that group, shaded regions are 95% confidence intervals.

Training Trials:

We conducted an ANOVA with the same trial set factors as the previous experiment and the group factors of pause and no-cursor. We found an effect of trial set [$F(3,234)=444.85$, $p<.001$, $\eta^2=.81$] and an interaction between trial set and group [$F(6,234)=27.50$, $p<.001$, $\eta^2=.20$]. These effects seem to be driven by the slower learning and much smaller rebound in the no-cursor paradigm. Follow-up t-tests show a significant difference between the pause and no-cursor group during R1, R1_late and R2 trials sets with $p<.001$. However, both groups performed similarly by the end of the error clamp phase [$t(45.98)=1.49$, $p=.144$]. These results once again suggest that active movements between training trials interferes with learning.

Model Fitting:

Figure 3B shows the emergence of the implicit reach aftereffects along with the model's proposed slow process. Visually it is clear the slow process predicted by the model does not match the pattern of the reach aftereffects. In all our model simulations, the slow process rises slowly and continues to increase throughout training. This is not the pattern we see with the reach aftereffects.

Testing Trials:

We also looked to see the speed at which reach aftereffects develop. We found reach aftereffects were present at the first trial set, after only 1-4 rotated training trials [$t(47)=20.28$, $p<.001$, $d=2.92$, $\eta^2=.79$, 10.85°]. These aftereffects continued to increase another 5.67° by the end of the first rotation [$t(47)=5.29$, $p<.001$, $d=.76$, $\eta^2=.18$]. A closer look at no-cursor performance during rotated-cursor training revealed a significant difference between the first (trials 65-68) and second (trials 69-72) trial sets [$t(47)=3.22$, $p=.002$, $d=.46$, $\eta^2=.07$, 2.96°]. Reach aftereffects continued to increase

slightly during the rest of training [$t(47)=2.46$, $p=.018$, $d=.35$, $\eta^2=.03$, 2.71°]. However, this further increase following the initial first trial set was so small that there was no significant change between each set of 4 trials to the next for the subsequent 20 rotated trials (trial range 68-88) $p>.19$. Thus, almost the entire change in no-cursor reaches, i.e., the implicit reach aftereffects, rapidly occurs within the first four trials.

Implicit Measures of Learning:

As both reach aftereffects and hand localization shifts are thought to be implicit and potentially driven by similar processes we compared the first test trial after the first rotated training trial and found no significant difference between the reach aftereffects, and either of the active [$t(73.54)=-1.08$, $p=.28$] or passive [$t(59)=-1.81$, $p=.08$] localization test trials. We speculate that these initial reach aftereffects may mainly reflect the changes in hand estimates, or a similar training signal (6,15,25), before additional sources of information emerge to contribute even larger shifts in reach aftereffects and no further shift in hand localizations.

Speed of Learning:

While tangential to the main goal of this study, we found that intervening trials that involve active movements (no cursor, or active localization where participants moved their own trained hand) slowed down learning when compared to just passive hand displacements or a pause in time. We can in fact predict for individual participants whether they made self-generated movements in the interleaved testing trials or not for 114 / 144 participants (79%; chance=80/144 or 55%; $p<.001$ binomial exact test) based on a multiple logistic regression model without interactions, using the parameters of the two-rate model as predictors. This shows that learning is slowed by having active intervening movements made in the absence of visual feedback.

Discussion

While many studies measure and model the time course of reaches in response to a perturbation (19,26), very few investigate the emergence of other outcomes of training, such as reach aftereffects and changes in estimates of hand position, but see: (20,21,27). In the current study, we measure implicit changes as reach aftereffects and estimates of passively and actively displaced hand position, at high temporal resolution. This is accomplished by interleaving every reach training that has aligned, rotated or error-clamped cursor feedback with one test trial. We test whether the pattern of implicit changes can be explained by, or even contribute to, different processes that are widely used to describe the rate of adaptation. We find that reach aftereffects and changes in estimates of hand position emerge and saturate rapidly during adaptation training. This suggests that implicit learning does not follow explicit changes and plays an important role in initial learning. In addition, this pattern does not match either the slow or the fast processes that account for the pattern of adaptation when reaching with a perturbed cursor. Indeed, changes in hand-localization can best be explained as a proportion of the visual-proprioceptive discrepancy experienced on the previous trial only. These

inconsistent patterns of emergence may indicate that the slow process is not synonymous with either of these well-established implicit components of motor learning. Thus, while a two-rate model may be able to describe patterns of performance during visuomotor training in the current form, the slow process does not equal implicit processes.

As expected, reach performance with a rotated cursor for all four groups adhered well to a model that consists of a fast and a slow process (19). Yet, the pattern by which both changes in estimates of hand position and no-cursor reaches arose did not mimic the slow process. Similarities might have been expected since these processes have been proposed to reflect mainly the implicit component of learning (2,5,7,19,28). Likewise, while the measured changes in hand estimate and no-cursor reaches arose quickly, not surprisingly they didn't decay as would be expected by a process that would forget quickly. This suggests these model processes may not reflect observable behaviours and the slow process is not implicit learning as we have been measuring it.

Estimates of hand location are incredibly quick to shift, with participants only having to experience one rotated training trial to elicit the full shift. Hand localization responses are thought to measure the brain's state estimate of hand position and likely rely on at least two signals: an efferent-based predictive component and an afferent-based proprioceptive component, that both change during visuomotor rotation training (29,30). Since the two-rate model does not include a state estimation process per se, perhaps it makes sense that it cannot explain proprioceptive recalibration. We see here that a proportional fit seems to explain changes in hand estimates throughout the adaptation task, especially during the error-clamp phase where the size of the visual-proprioceptive discrepancy is determined by the size of the reach deviation. The pattern of change in estimates of hand location points to this process being independent of the other processes of motor learning.

The two signals thought to contribute to changes in hand location, prediction and proprioception, may be differentially involved in active and passive localizations (29,30). Active hand localization exhibits slightly larger shifts than passive hand localization. This difference in size of localization shift is known and can be attributed to the additional information provided by self-generated movement that allows the efferent-based, predictive component (29,30). Regardless, the size of the errors in hand localization are consistent with previous studies that – after many more trials – observe changes in felt hand position between 20-30% of the rotation (14,20,21,23,31), which scales with the size of the rotation in some circumstances (24). Importantly, the proportional account explains these differences and still describes the localization data well.

Reach aftereffects also emerge incredibly quickly, while not reaching asymptote as fast as shifts in hand localization. The similar size of aftereffects and hand localization shifts after just one rotated training trial potentially indicates a shared source. In addition, participants who perform no-cursor reaches with minimal instruction or more detailed instruction (to ensure strategy wasn't used) show similar rates and

extents of learning of reach aftereffects. If no-cursor reach deviations reflect implicit changes in state estimation, these arise much quicker than previously thought bolstering recent claims that the earliest wave of muscle activity during adaptation is influenced by implicit motor learning (32).

Conclusion

The two-rate model fits visuomotor adaptation data excellently. We suggest here that the conventionally implicit components of motor learning; changes in estimates of hand location, and no-cursor reach deviations, do not follow the pattern of the two-rate model's slow process, nor indeed the fast process. The fast emergence of reach aftereffects and changes in hand estimates indicate implicit components of motor learning appear before or alongside explicit components of learning. Perhaps implicit processes lead or drive motor learning, unlike previously believed, but certainly they do not lag behind explicit processes. In addition, our results provide further evidence that implicit learning consists of at least two sub-processes that separately contribute to adaptation.

Methods

Participants

144 (mean age=20.31, range=17- 46, females=102) right-handed, healthy adults gave informed, prior consent to participate in this study. All procedures were approved by the York Human Participants Review Subcommittee. *Apparatus*

The experimental set-up is illustrated in Figure 4. While seated, participants held a vertical handle on a two-joint robot manipulandum (Interactive Motion Technologies Inc., Cambridge, MA, USA) with their right hand such that their thumb rested on top of the handle. A reflective screen was mounted horizontally, 14 cm above the robotic arm. A monitor (Samsung 510 N, 60 Hz) 28 cm above the robotic arm presented visual stimuli via the reflective screen to appear in the same horizontal plane as the robotic arm. A Keytec touchscreen was placed above the robotic arm and was used to record reach endpoints of the left hand, to unseen, right hand targets (see (14) for more details). Subject's view of their training (right) arm was blocked by the reflective surface and a black cloth, draped over their right shoulder. The untrained, left hand was illuminated, so that any errors in reaching to the unseen, right target hand could not be attributed to errors in localizing the left, reaching hand.

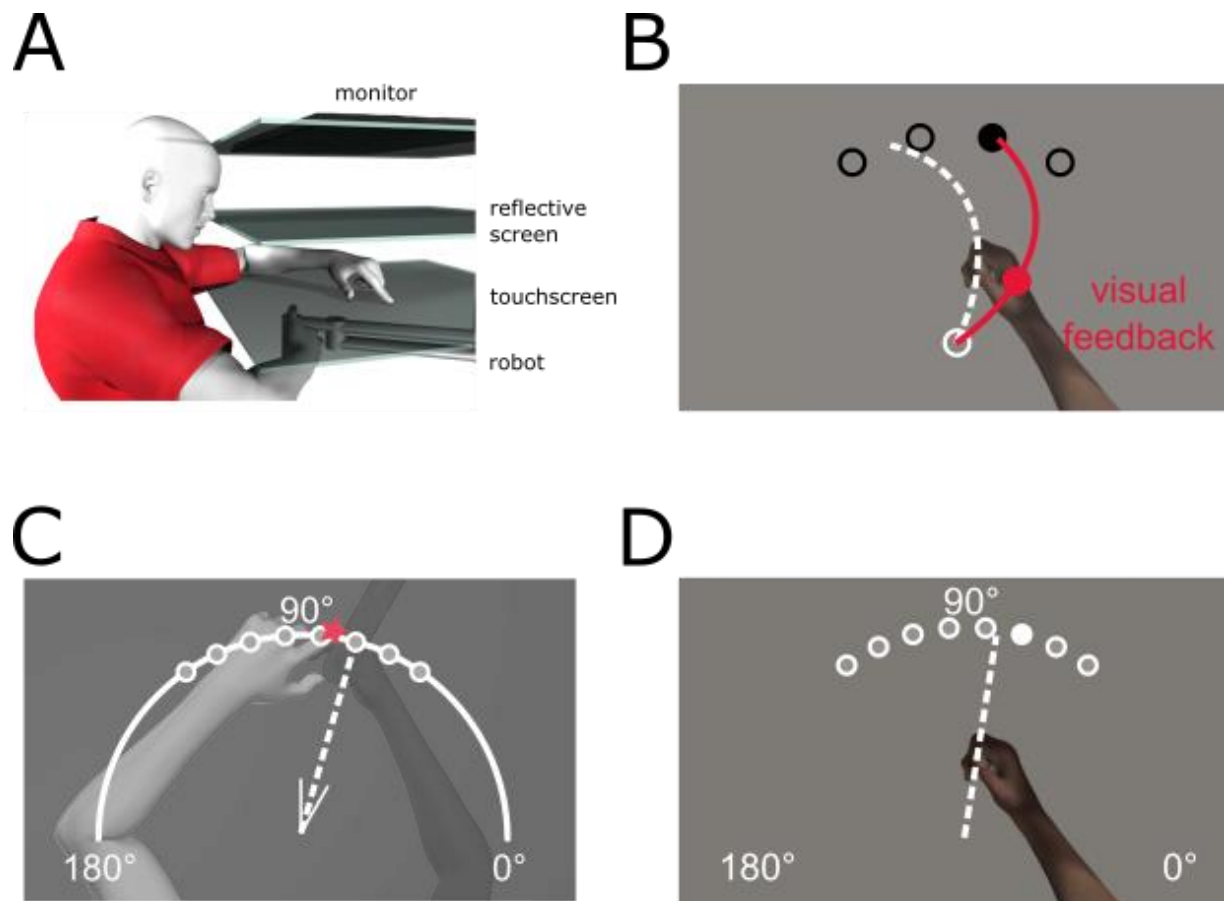


Figure 4. Experimental setup and design. **A:** Side view of the experimental set-up. The top layer is the monitor, middle layer is the reflective screen, and the bottom opaque layer is the touchscreen. The robot is depicted beneath with the participants' right hand grasping it. **B-D:** Top views of task specific set-ups. **B: Training (and Clamp) trial.** The home position is represented by a green circle with a 1 cm diameter; located approximately 20 cm in front of the subject and not visible during the trial. Targets are represented by white circles with a 1 cm diameter located 12 cm radially from the home position at 60°, 80°, 100° and 120°. Participants hand cursor was also a 1 cm diameter blue circle. **C: Localization test trial.** Participants were either passively moved to one of the eight target locations, or actively moved their hand in the direction suggested by the white wedge at the home position, these real and suggested locations include 55°, 65°, 75°, 85°, 95°, 105°, 115° and 125. The participants then used the index finger of their left untrained hand to indicate the felt location of the right hand (specifically the thumb). **D: No-cursor test trial.** Participants made ballistic reaches to one of 8 target locations without any visual feedback of their movement.

Trial Types

Reach-training trials

Participants, regardless of group, reached as accurately as possible with their right hand to one of the four possible target locations (see figure 4B). In all reaching trials, i.e., with cursor, with clamped cursor and with no cursor, participants had to reach out 12 cm from the home position to a force cushion within 800 ms. Participants received auditory feedback throughout training indicating if they met the distance-time criteria or not. The target would then disappear, and the robot manipulandum returned

the right hand to the home position where they wait 250 msec for the next trial. The hand cursor was aligned with the hand for the first 64 training trials, then rotated 30° CW for 160 training trials and then rotated 30° CCW for 16 training trials. This was followed by 48 error-clamped trials, dashed lines in Fig 5, which were identical to the reach training task except that the cursor always moved on a straight line to the target. The distance of the error-clamped cursor from the home position was identical to the distance of the hand from the home position.

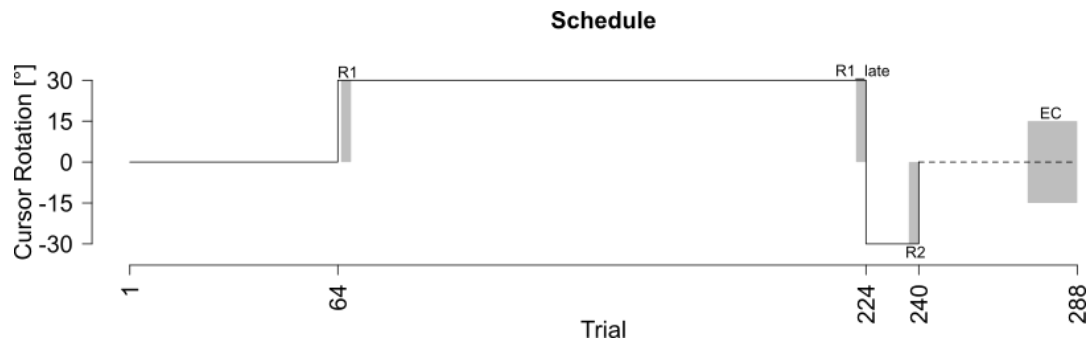


Figure 5. Experimental Schedule. Participants reached to visual targets with a perturbation denoted by the black line. The dotted line at the end of the paradigm signifies clamp trials where there was no visual error as the cursor always moved to the target regardless of the participants movement direction. Trials included in analysis are as follows: R1=trials 65-68; R1_Late=trials 221-224; R2=trials 237-240; EC=273-288.

Test trials

Participants switched between two tasks, the first of the two tasks was either reach-training or clamp-trials whereas the second trial was one of four possible test trials, each one performed exclusively by participants in one group. These test trials were: (1) localization of the unseen hand position when the hand was passively moved by the robot, “Passive localization”, N=32, (2) localization of the unseen hand after it was actively moved by the participant, “Active localization”, N=32, (3) a no-cursor reach to a target, “No-cursor”, N=48, or (4) a short pause phase with no hand movement, “Pause”, N=32, serving as a control group. After each test trial, the robot returned the participants’ hand back to the home position.

Hand localization

Two of the four experiments involved measuring estimates of unseen hand location in order to assess different components of state-estimation. For both localization trials (Fig 4C), a white arc would appear on the screen, spanning from 0° to 180°, the arc was 12 cm away from the home position. Then the hand was either passively displaced by the robot to one of the eight target locations (passive localization) or the hand movement was self-generated by the participant (active localization). Passive movement of the hand took 650 ms to cover the 12 cm distance. In active localization trials, participants chose their own hand-target location. They were guided with a small wedge that appeared at the home position spanning 30°, the center of the arc was on the passive localization target locations. This active, self-generated

movement was stopped by a force cushion at the 12 cm mark. Regardless of localization trial type once their right, unseen target hand was locked in place, participants used their visible, left index finger, to indicate on the touchscreen, along this arc, where they believed their right, stationary, unseen hand was. The arc was continuously visible until the touchscreen registered the participants estimate.

Reaching without a cursor

Another test trial required participants to reach out, again 12 cm, to one of eight targets (Fig 4D) without a cursor representing their hand. The same distance-time criteria as in reach-training applied but without reinforcing sounds. This group originally had 32 participants who were simply told that there would be no cursor for these trials. We later add 16 more participants who were specifically told not to include any learned strategy. Since the results did not differ between these two sub-groups, (see R notebook for details: <https://osf.io/9db8v/>), the results were collapsed for analyses.

Data Analysis

We analyzed the two groups with localization test trials together and no-cursor test trial groups, we always included the pause group with each of the analysis as a control version. The reach training trials, localization trials and no-cursor trials were analyzed separately from each other.

Reaching with a cursor and clamp trials: To quantify reach performance during training, the angular difference between a straight line from the home position to the target and a straight line from the home position and the point of maximum velocity is computed.

Hand Localization: Estimates of hand location in both the passive and active localization groups were based on the angular endpoint error between the movement endpoint of the right unseen hand and the left hands responses on the touchscreen.

Reaching without a cursor: To determine if participants exhibit reach aftereffects as a result of training, we measured reach endpoint errors during no-cursor trials. The reach error is calculated based on the angular deviation between the reach endpoint and the target location, relative to the home position.

Analyses

All data was visually screened for incorrect trials and outliers of more than three standard deviations across participants within each trial were deleted, resulting in 2.2% of the data being removed. All measures were normalized, by subtracting out each subjects' performance during the second half of the aligned session (e.g. trials 32-64). To quantify changes in training and test trials we conducted ANOVAs consisting of a within-subjects factor of trial set and a between-subjects factor of group. The trial-set factor consisted of four levels which were an average of: the first 4 rotated trials (R1), the final 4 trials from the first rotation (R1_Late), the final 4 trials from the second rotation (R2) and the last 16 trials from the clamp phase (EC). Significant main effects and interaction were followed-up by pairwise comparisons. All results are reported with a Welch t-tests and an alpha of .05.

Modeling

We fitted the two-rate model (22) to our data. This two-rate model is composed of a slow process that slowly increases over time until it is the driving force of performance, and a fast process that rises quickly but eventually decays back to zero. The sum of these two processes determines the overt behaviour and can explain the rebound seen in the error-clamp phase. During error-clamps, neither process learns, but the fast process will forget how it adapted to the counter rotation, while the slow process still exhibits part of its adaptation from the long initial training, resulting in a rebound.

This model postulates the reaching behavior exhibited on trial t (X_t), is the sum of the output of the slow ($X_{s,t}$) and fast process ($X_{f,t}$) on the same trial:

$$X_{t1} = X_{s,t} + X_{f,t}$$

Both of these processes learn from errors on the previous trial (e_{t0}) by means of a learning rate (L_s and L_f), and they each retain some of their previous state ($X_{s,t0}$ and $X_{f,t0}$) by means of their retention rates (R_s and R_f):

$$X_{s,t1} = L_s * e_{t0} + R_s * X_{s,t0}$$

$$X_{f,t1} = L_f * e_{t0} + R_f * X_{f,t0}$$

The model is further constrained by making sure the learning rate of the slow process is lower than that of the fast process: $L_s < L_f$, and by having the retention rate of the slow process be larger than that of the fast process: $R_s > R_f$.

All model fitting was done on the mean angular reach deviation at peak velocity during all training reaches (disregarding target location). The error term was set to zero during the final error clamp phase of the experiment, as the participant did not experience any performance error. The model was fit in R (33) using a least mean-squared error criterion on the six best fits resulting from a grid-search. The parameter values corresponding to the lowest MSE between data and model was picked as the best fit, and this was repeated for all groups. The datasets for the current study are available on Open Science Framework, <https://osf.io/9db8v/>.

Acknowledgements:

This work was supported by a Canadian Network for Research and Innovation in Machining Technology NSERC Operating grant (DYPH) and the German Research Foundation (DFG) under grant no. HA 6861/2-1 (BMtH). The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Competing interests:

The author(s) declare no competing interests.

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